# PRIMARY NON-DISJUNCTION IN DROSOPHILA HYDEI.*

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## INTRODUCTION.

Non-disjunction of the sex chromosomes has been recorded in several species of Drosophila. Bridges ('13) studied this phenomenon first in Drosophila melanogaster. A review of his work and that of other investigators is given by Morgan, Bridges, and Sturtevant ('25), with citations of papers published up to that time. In Drosophila simulans non-disjunction has been reported by Sturtevant ('21). Weinstein ('22) recorded its occurrence in Drosophila virilis and Lancefield and Metz ('21) have studied it in Drosophila willistoni. Recently Timofeeff-Ressovsky (work unpublished) has observed non-disjunction in Drosophila funebris.

From the standpoint of comparative genetics it seemed worth while to undertake a study of this phenomenon in Drosophila hydei. Furthermore the limited investigation of the species had resulted in the finding of several sex-linked mutants which gave promise of being unusually favorable tools in a study of this kind.

Reference to Figure 1 will show the tentative map of the x-chromosome and the mutants used. In order to represent the genetic map on a larger scale a long section of the map has been omitted as indicated by the break in each chromosome shown. The x-chromosome of this species is actually a long V-shaped structure according to the cytological investigation of Metz and Moses ('23).

Notched (N) at locus 0.0 was found by Spencer ('27). It is a dominant wing mutant, causing a thickening of the wing-veins, notching of the margins of the wings, and a lethal effect in males. It is presumably lethal also in homozygous females, though in the nature of the case a homozygous female could only be produced through equational non-disjunction as there are no Notch males to pass the factor on to their daughters.

*Presented at the meeting of the Ohio Academy of Science, April 18, 1930.

White (w) at 3.6, and vermilion (v) at 15.1 are recessive eye color mutants found by Clausen ('23).

Bobbed (b) at 62.6 was reported by Clausen ('23), and an allelomorph ($b^2$), was recorded by Spencer ('27). Clausen's bobbed was used in this study. Bobbed is characterized in homozygous females by a reduction in the size of the bristles and hairs in all parts of the body, and in Clausen's allelomorph by abnormalities in the pigment bands of the abdomen in some flies. It is ordinarily sex-limited. The male, which transmits the bobbed gene in its x-chromosome is entirely normal in appearance. Bobbed mutants, parallel both in the position of their loci in the x-chromosome and in being sex-limited are known in Drosophila melanogaster and in Drosophila simulans. In the latter it is the female which is normal in appearance. In an extensive and brilliant series of researches Stern ('26a, '26b, '27, '29a, '29b) has shown through the study of non-disjunction and other chromosome aberrations involving this mutant that the sex-limited nature of the mutant in Drosophila melanogaster is due to the presence of a bobbed suppressor or normal allelomorph in the Y chromosome. His work has not only demonstrated the presence of this inhibitor in the Y, but has shown it to be limited to a certain region of the Y-chromosome.

In work on the linkage of bobbed in Drosophila hydei (Spencer '27) a male showing the bobbed character in extreme degree was recorded and interpreted as a gynandromorph. This individual was sterile. Stern ('29b) has recently referred to this individual and analysed the case not as a gynandromorph, but as being due to non-disjunction in the male parent resulting in a sperm carrying neither X nor Y-chromosome, which on fertilizing an X-bearing egg produced this male with X composition and sterile through lack of the Y-chromosome.

## PROCEDURE AND RESULTS.

As shown in Figure 1 females heterozygous for Notch, homozygous for white and bobbed, and carrying the wild-type allelomorphs at the vermilion loci were mated to males carrying the wild-type allelomorphs for Notch and white at their respective loci, the vermilion and bobbed genes in their X-chromosome, and presumably carrying the bobbed suppressor in the Y-chromosome. From such a cross three classes of offspring would be expected to occur in about equal numbers:

white-eyed, normal-winged, phenotypically normal-bristled males; mahogany-eyed (wild-type), Notch-winged, bobbed-bristled females; mahogany-eyed, normal-winged, bobbed-bristled females. Reference to Figure 1 will make this clear. The fourth genotypic class, the white Notch males do not appear among the phenotypes, due to the lethal action of Notch. Table 1 gives the actual results of counts of the offspring from 146 cultures of the above cross.

TABLE I.

THE OFFSPRING FROM 146 SINGLE MATING CULTURES OF NOTCH, WHITE, BOBBED FEMALES TO VERMILION, GENOTYPICALLY BOBBED MALES.

| Phenotypic Classes | Number of Flies |
|---|---|
| White-eye, normal-wing, normal-bristle males | 4,735 |
| Mahogany-eye, normal-wing, bobbed-bristle females | 5,067 |
| Mahogany-eye, Notch-wing, bobbed-bristle females | 4,482 |
| White-eye, Notch-wing, normal-bristle females | 7 |
| Vermilion-eye, normal-wing, extreme bobbed males | 3 |
| White-eye, normal-wing, extreme bobbed male | 1 |
| White-eye, normal-wing, normal-bristle female | 1 |
| Vermilion-eye, normal-wing, bobbed-bristle female | 1 |
| Total Flies | 14,297 |

EXPLANATION AND DISCUSSION.

In Table 1 of the total of 14,297 offspring all but 13 belong to the classes expected. The three expected classes occur in approximately a 1 : 1 : 1 ratio. As is usually the case in counts involving Notch this class is somewhat lower than the others, due to a lessened viability of the Notch flies. It should be stated that the bobbed character is not always easy to identify in females and there is some tendency to overlapping of the wild-type. However, in most of the individuals it could be distinguished and all females of the mahogany Notch and mahogany normal-winged classes have been classed as penotypically bobbed.

The seven white-eyed, Notch-winged, normal-bristled females and the three vermilion-eyed, normal-winged, extreme bobbed males are due to non-disjunction of the X-chromosomes of the female parent. This is made clear by reference to Figure 2. In non-disjunction of the reductional type the two X-chromosomes of the primary oocyte may either go into the second-

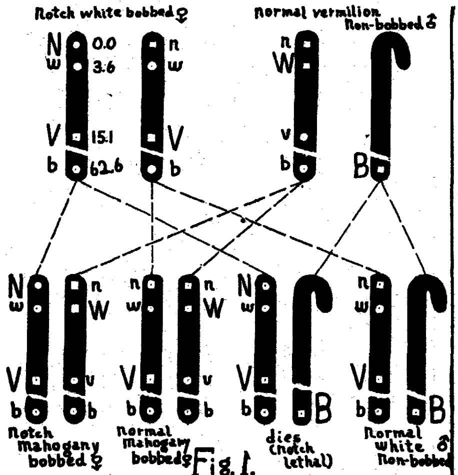

Fig. 1.

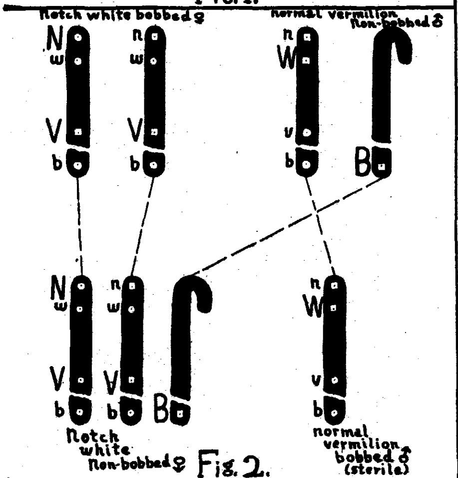

Fig. 2.

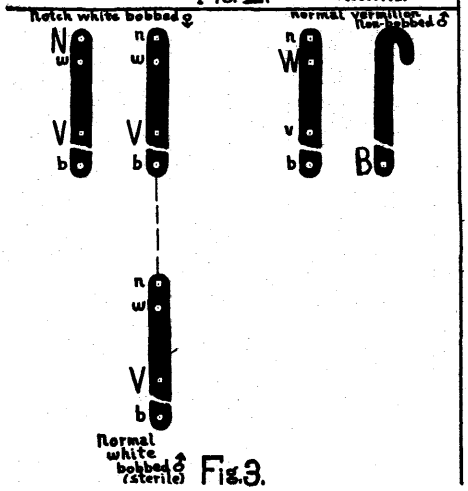

Fig. 3.

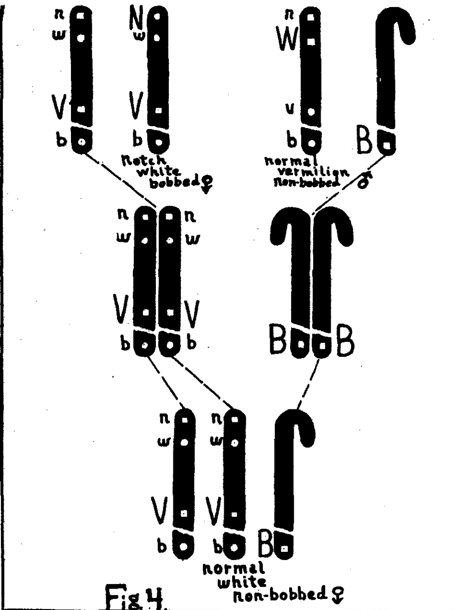

Fig. 4

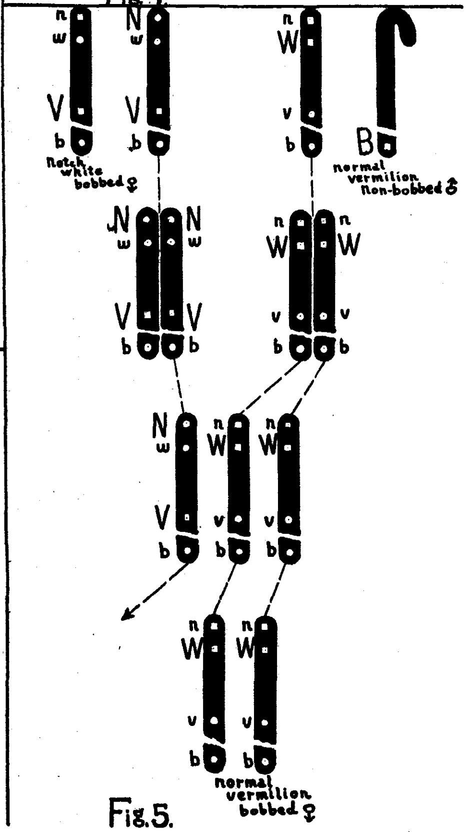

Fig. 5.

ary oocyte together or they may be expelled together into the first polar body, leaving the secondary oocyte without any X-chromosome. When an egg containing the two X-chromosomes of the mother is fertilized by a Y-bearing sperm a female is formed, with an XXY constitution as indicated by the offspring to the left in Figure 2. These females are Notch and white-eyed like their mothers, but as they each carry a Y-chromosome they are not bobbed like their fathers. When an egg without either X is fertilized by an X-bearing sperm a male is produced, XO in composition, vermilion-eyed and normal-winged like the father, but showing the bobbed character as the Y-chromosome with its bobbed suppressor is not present. The genotype of such an individual is shown to the right in Figure 2. In Drosophila melanogaster it has been shown that XO males are always sterile. The three vermilion, extreme bobbed males were mated each to several sisters but all proved to be sterile. Thus the XO composition of these males is shown by their eye-color, their possession of the bobbed character in extreme and unmistakable form, and their sterility.

The explanation of the one white-eyed, extreme bobbed male is to be found in Figure 3. In this case non-disjunction in the male parent resulted in the formation of a sperm with neither X nor Y-chromosome present. When this sperm fertilized an egg bearing a single X with the white, normal-

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EXPLANATION OF FIGURES.

Fig. 1. The sex-chromosome composition of a Notch, white, bobbed female and a normal-winged, vermilion, phenotypically non-bobbed male and of the classes of offspring to be expected from them when normal disjunction of the sex-chromosomes occurs in both parents.

Fig. 2. The two classes of offspring resulting from primary non-disjunction of the reductional type. The XXY female produced by fertilization of an XX egg by a Y sperm and the XO sterile male coming from the fertilization of an egg bearing no X by a sperm carrying an X.

Fig. 3. A sterile male produced by primary non-disjunction of the reductional type in the male parent. An X-bearing egg fertilized by a sperm carrying neither X nor Y and due to reductional non-disjunction in the male parent.

Fig. 4. An XXY female due to primary non-disjunction of the equational type in the female parent.

Fig. 5. A patroclinous female receiving her two X chromosomes from the male parent as a result of equational non-disjunction in this parent followed by the elimination of the maternal X as shown by the arrow.

NOTE.—The X chromosome is represented as a straight rod, the Y chromosome as a hooked rod. The break in the chromosome represents a long section of the genetic map left out. The squares represent the normal or wild-type factors or genes and the circles the mutant factors.

winged and bobbed genes in it a male of the above phenotype was produced. This XO male was sterile. The use of the bobbed mutant makes it possible to detect non-disjunction in the male. If the bobbed character were not being followed non-disjunction could occur in the male without detection, as individuals from non-disjunction sperm would not differ phenotypically from those which had come from ordinary sperm. Stern ('27, '29b) has recorded non-disjunction in the male in bobbed stocks of Drosophila melanogaster.

The one white-eye, normal-winged, normal-bristled female is accounted for by equational non-disjunction of the not-Notched chromosome of the female parent as shown in Figure 4. Equational non-disjunction, while not as common as that of the reductional type, has been repeatedly recorded in Drosophila melanogaster. In the present instance the heterozygous Notched condition of the female parent makes it certain that the non-disjunction was of the equational type. A possible alternative explanation of this individual would be that of gynandromorphism. The not bobbed condition might then be due to normal overlapping of the bobbed character. The female might have received one X-chromosome from the father and one from the mother. The paternal X might have been eliminated from an early cleavage cell, from which all eye tissue developed. This would give a gynandromorph, female posteriorly and male and with white eyes anteriorly. Such a gynandromorph would, however, have produced sons half of which would have been white and the other half vermilion. This female on being bred produced only white-eyed sons, showing that she was homozygous for white. This fact proved that both her X-chromosomes were derived from her mother. They must have come from the not-Notched X through non-disjunction at the equation division, as the fly was not Notched.

That none of the seven Notched white females recorded above were due to equational non-disjunction of the Notch bearing chromosome was shown by breeding tests. Had any of the above flies been homozygous for Notched through equational non-disjunction they should have given only Notched daughters and no sons at all. As none of them gave this result on breeding it seems clear that each of the seven was due to reductional non-disjunction. This is in accord with the implication that homozygous Notched females would be lethal as are Notched males.

The patroclinous vermilion-eyed, normal-winged, bobbed female presents some difficulties. In Figure 5 a formal explanation of how such an individual might have occurred is given. It must be supposed that equational non-disjunction has occurred in the male, resulting in a sperm with two paternal X-chromosomes. This sperm fertilizes either an egg which through non-disjunction lacks an X or an X-bearing egg. In the latter case there is elimination of the maternal X soon after fertilization resulting in a female homozygous for the sex-linked factors of her father. The simultaneous occurrence of non-disjunction in male and female gametes seems an event so extremely rare that we may disregard it in favor of the alternative of non-disjunction in the male followed by somatic elimination of one of the three X-chromosomes (in this case the one maternal X) from the zygote. While there is little evidence on the point it would not seem unlikely that the presence of an extra X-chromosome in the zygote might favor the loss of an X during an early cleavage stage. Mrs. L. V. Morgan ('22) has shown that the female from which the double yellow stock with attached X-chromosomes has been derived was a mosaic due to somatic elimination of the maternal X from a fly which had arisen from an equational non-disjunction sperm fertilizing an X-bearing egg. She cites two additional cases (L. V. Morgan '29) in Drosophila melanogaster in which this sequence of events has occurred. The alternative explanation of gynandromorphism in our present case was shown to be invalid by breeding tests. All sons from this female were vermilion showing that the fly was homozygous vermilion.

The data presented here give about one individual in 1100 from primary non-disjunction of the sex chromosomes. This is a somewhat higher percentage than that given for Drosophila melanogaster by Morgan, Bridges and Sturtevant ('25). However, the data in our present study are insufficient to give an accurate idea of the relative frequency in the two species. Mrs. Morgan ('29) has suggested that Notched and bobbed may both tend to increase non-disjunction. Whether this be true or not they do favor its study and analysis. It is significant to find that primary non-disjunction in this species gives rise to essentially the same phenomena, especially in the case of bobbed, as are found in Drosophila melanogaster.

Secondary non-disjunction is at present being studied in this species and will be reported on at a later date. It may be said that the secondary exceptions are apparently of a much lower frequency than in other species studied.

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## NEW REPORT ON NEW BRUNSWICK.

The Canadian Department of the Interior has just issued a beautifully printed and illustrated report on New Brunswick of 166 pages, with 33 photographs, 10 sketch maps and a general map in color. "The potentialities of this maritime province have undoubtedly been overlooked during the period of the agricultural development of Western Canada and the industrial growth of Ontario and Quebec, for it is only recently that its water-powers and forest wealth have been utilized in large-scale pulp and paper enterprise. Progress in this direction has indeed been remarkable. Last year the largest power site in the Maritimes was developed at Grand Falls, with an installation of 60,000 horse-power and transmission line of 104 miles to Chaleur Bay; 5,500 horse-power was added to the 9,000 horse-power already developed on the Nipisiguit; the capacity of the plants at Edmundston and Bathurst were enlarged; while a newsprint mill with an initial daily capacity of 250 tons came into operation in March, 1930; and a bleached sulphite mill at Athol has lately been completed.

"A similar awakening is in evidence in regard to the fertile and cheap agricultural lands, minerals and fisheries, and the many recreational attractions of the province, all of which resources and the development opportunities they present are dealt with in this governmental publication, which can be obtained from the Director, Natural Resources Intelligence Service, Department of the Interior, Ottawa."